

The effect of habitat conditions on the abundance of populations and selected individual and floral traits of *Impatiens glandulifera* Royle

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Abstract: The effect of site conditions on the abundance of populations of *I. glandulifera*, selected individual features (height and width of stems, number of whorls and side branches, flower production), and floral traits (total length of flowers, length and width of lower sepal, spur length) were investigated in years 2013-14. Observations were conducted on fallow land, at roadsides, along riverbanks and edges of a riparian forest as well as in a willow thicket and a riparian forest inside located in the Vistula River valley in southern Poland. In these stands, taken successively, light availability gradually diminished, while plant canopy height and soil moisture increased. The low abundance of the population on the fallow land may have been caused by low soil humidity triggering seedling mortality, whereas the low abundance in the interior of the riparian forest may have been due to seasonal water stagnation hampering the development of offspring. The increasing values of individual traits from the fallow land to riparian forest edge might be linked to growing lateral shade, whereas the much lower values in the willow thicket and forest interior might be caused by full shade. Individuals growing on the fallow land, at roadsides, and along riverbanks produced flowers with small total lengths and large lower sepals and spurs, whereas individuals occurring in willow thickets and riparian forests showed opposite tendency. The considerable stem dimensions and substantial production of large flowers may augment chances for successful resource capture and pollinator visits in open sites, while the reduced size of individuals and moderate production of small flowers may be sufficient for the maintenance of populations in closed habitats.

Key words: abundance, flower, individual, *I. glandulifera*, population, stem, traits

1. Introduction

Alien invasive plants represent a major threat to native biodiversity and the functioning of invaded ecosystems (Vitousek *et al.* 1994; Mack *et al.* 2000; Winter *et al.* 2009). Currently, the Himalayan balsam (*I. glandulifera* Royle) is among the most invasive annual plants in Europe (Lambdon *et al.* 2008). This species is one of the tallest alien weeds, reaching up to 2-3 metres under favourable conditions. The stem of this species, divided into nodes and internodes, is thick and hollow. Lanceolate-serrate leaves on the main stem grow in whorls, while leaves on side stems are arranged in an alternating manner. The umbel-shaped inflorescences contain 2-14 pink, white or purple flowers (Berling & Perrins 1993; Clements *et al.* 2008). Irregular in shape,

the protandrous flowers exhibit dorsiventral symmetry. They are characterised by broad petals, small lateral sepals and a saccate lower sepal with a short recurving spur. The androecium and stigma are suspended downward from the roof of the lower sepal. The dorsal petals form a hood above the androecium, whereas the lower petals serve as a platform for landing insects. To obtain nectar, insects crawl along the lower sepal to the posterior spur and usually exit flowers covered with pollen. Among the main visitors are species from the *Bombus*, *Apis* and *Vespa* genera (Titze 2000; Nienhuis & Stout 2009).

I. glandulifera, which originated in the Himalayas and East India, is a widely naturalised alien plant rapidly invading waste land across all of the continental Europe, Britain and Ireland. Most frequently, it occurs along

rivers and in flood plain vegetation, mostly in willow bushes and alluvial willow-poplar forests, as well as in tall herb fringe communities (Balogh 2008).

To date, investigations on *I. glandulifera* have focused on mechanisms of seed germination (Jouret 1977), variability of selected individual and population traits (Kollmann & Bañuelos 2004; Willis & Hulme 2004; Chmura *et al.* 2013; Kostrakiewicz-Gierałt & Zając 2014), genetic diversity of populations (Zybartaite *et al.* 2011), the effect of invasion on resident plant communities (Hejda & Pyšek 2006; Hulme & Bremner 2007; Hejda *et al.* 2009; Gruntman *et al.* 2014), and associated invertebrate communities (Tanner *et al.* 2013).

Despite growing interest in this species, the present state of knowledge is still insufficient; accordingly, the present investigations on the influence of site conditions on the abundance of populations and selected individual and floral traits were performed. Specific aims included observations of the impact of neighbouring plants height, light availability and soil humidity on: (1) the number and density of individuals; (2) the variability of chosen traits of individuals, such as the height of stems, width of stems at soil level, number of whorls with side branches, number of side branches and total number of flowers; (3) the variability of selected floral traits, i.e. total length of flowers, length and width of lower sepals and spur length.

The working hypotheses were the following: (1) the number and density of individuals would differ among habitats; (2) the individual traits would reach greater values in shaded sites, than in sun-illuminated places; (3) the floral traits would not differ among observed sites.

2. Study area

The study area was located in south-western part of Kraków (Southern Poland), where several limestone monadnocks (Jurassic-Cretaceous) and tectonic depressions of the Brama Krakowska gate occur (Kondracki 2000). The geological structure and diverse hydrological conditions contributed to the formation of various types of soils. Rendzinas occur on the limestone and chalk hill slopes, brown soils – at the foot of the hills, black earth and light clay – in the tectonic depressions, whereas alluvial soils – in the vicinity of river beds (Skiba *et al.* 2005; Drewnik *et al.* 2007). In the study area, a wide spectrum of plant communities was observed: from willow thickets and riparian forests in close vicinity of river beds, through moist meadows in the terrain depressions and xerothermic calcareous grasslands on hill slopes, to ruderal communities appearing near buildings and along edges of roads (Dubiel & Szwaگرzyk 2008).

3. Material and methods

3.1. The studies of habitat conditions

The investigations were carried out in 2013-14 in several sites located across the Vistula Valley from Pychowice to Tyniec (Fig. 1). All study sites represented different plant communities invaded by *I. glandulifera* individuals. These included fallow land, roadsides, riverbanks, edges of a riparian forest, a willow thicket and the interior of the riparian forest. The average height of vascular plants in each location was evaluated on the basis of measurements of 30 randomly chosen stems (from ground level to the top) of different species (excluding *I. glandulifera*). The measurements were performed using a folding tape measure. The light intensity at the soil level was surveyed with a Voltcraft MS-1300 digital light meter (accuracy $\pm 5\% + 10$ digits; measuring range 0.01-50.000 lx). In total, 10 measurements per location were taken between 10 and 25 August 2013. All measurements were performed on sunny days. The light intensity in a given site was calculated by adding all values and dividing by the number of measurements. The soil humidity at ground level was evaluated on the basis of 30 measurements using a BIOWIN 071505 handheld soil moisture sensor (measuring range 1-10).

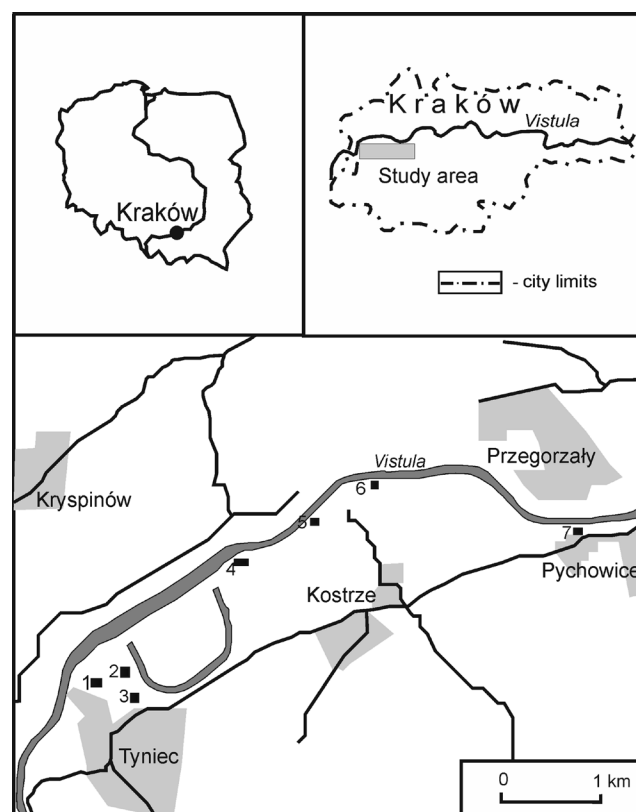


Fig. 1. Location of the studied populations of *Impatiens glandulifera*
 Explanations: 1 – fallow land, 2 – riparian forest interior, 3 – riparian forest edge, 4 – willow thickets, 5 – river bank 1, 6 – river bank 2, 7 – roadside

Table 1. Characteristics of habitat conditions in the studied localities of *Impatiens glandulifera* in the year 2013

Habitat	Fallow land	Roadside	River bank 1	River bank 2	Riparian forest edge	Willow thickets	Riparian forest interior
Site area (m ²)	130	80	90	70	120	150	130
No. of species per site	16	14	16	21	22	17	16
Dominant species (cover > 20%)	<i>Artemisia vulgaris</i> , <i>Lapsana communis</i> , <i>Galium aparine</i>	<i>Solidago canadensis</i>	<i>Rubus</i> sp., <i>Galium aparine</i>	<i>Impatiens parviflora</i> , <i>Melilotus albus</i>	<i>Robinia pseudoacacia</i> , <i>Fraxinus excelsior</i>	<i>Salix fragilis</i> , <i>Salix cinerea</i>	<i>Fraxinus excelsior</i> , <i>Acer negundo</i>
Subdominant species (cover 5-20%)	<i>Chenopodium album</i> , <i>Urtica dioica</i>	<i>Rubus</i> sp.	<i>Artemisia vulgaris</i> , <i>Aegopodium podagraria</i>	<i>Rubus</i> sp.	<i>Sambucus nigra</i>	<i>Urtica dioica</i>	<i>Sambucus nigra</i> , <i>Euonymus europea</i>
The mean (\pm SD) vascular plant cover (cm); N=30*	63.2 (\pm 17.3) A	126.2 (\pm 64.2) BC	109.3 (\pm 21.9) BC	178.2 (\pm 35.7) DE	183.7 (\pm 57.2) DEF	223.4 (\pm 68.9) EF	322.2 (\pm 68.1) G
The mean (\pm SD) light intensity at soil level (lx); N=30*	32 800 (\pm 8 100) ABC	31 100 (\pm 9 200) ABC	30 100 (\pm 3.900) ABCD	22 400 (\pm 9 500) CD	14 600 (\pm 6 400) EF	14 400 (\pm 2 600) EF	7 500 (\pm 1 200) G
The mean (\pm SD) soil moisture (range 1-10); N=30*	2.7 (\pm 0.4) AB	3.2 (\pm 0.8) AB	5.1 (\pm 1.3) CD	5.2 (\pm 0.9) CD	5.6 (\pm 0.4) CDEF	5.7 (\pm 0.4) CDEF	7.0 (\pm 0.5) G

Explanations: * – the value of statistical differences among the sites (the H Kruskal-Wallis test; $df=6$, $P < 0.001$) reached 142.9 in vascular plant height, 175.2 in light intensity, 171.2 in soil moisture. The different letters below values indicate significant differences among habitats

The statistical analysis, performed using the Kruskal-Wallis and post-hoc tests, showed that light availability gradually diminished in the aforementioned stands, while plant canopy height and soil moisture increased. A detailed description of habitat conditions is contained in Table 1.

3.2. The studies of population and individual traits

In years 2013 and 2014, the abundance of populations (the total number of individuals) of *I. glandulifera* was surveyed in each location. The mean density of individuals per m² was evaluated on the basis of the number of individuals occurring in 15 permanent square-shaped plots with dimensions 1m x 1m.

Then, in 2014, in each population, 30 individuals were randomly chosen for biometric studies of traits enabling effective resource capture and maintenance within a colonised site. These were: height and width of stems, number of whorls with side branches, number of side branches, and total number of flowers. The height of stems from the soil surface to the top of the stems

was measured using the folding tape, and the width of stems at ground level was measured using a Lux Tools Comfort digital caliper (accuracy \pm 0.01; measuring range 0.1-150 mm). Subsequently, 100 flowers were chosen at random to investigate the selected traits influencing the number of pollinator visits. These were: total length of flowers, understood as the distance between the top of the lower petal and the spur; maximal length of the lower sepal; width of the lower sepal in one-half of their length; spur length from the lower sepal base to the spur tip. A survey of analysed traits is given in Fig. 2. All floral traits were measured using a digital caliper.

Normal distribution of the untransformed data in the individual sample was tested using the Kolmogorov-Smirnov test, while variance homogeneity was ascertained using the Brown-Forsythe test at the significance level of $p < 0.05$. As the values of individual characteristics in some groups were not consistent with normal distribution and the variance was not homogeneous, the non-parametric Kruskal-Wallis and post-hoc test were used in the statistical analyses.

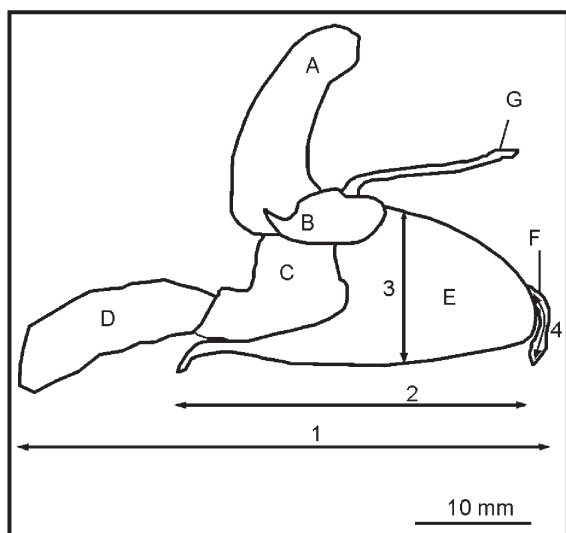


Fig. 2. The lateral view of *Impatiens glandulifera* flower (after Nienhuis, Stout 2009) showing the measured floral traits
 Explanations: A – dorsal petal, B – lateral sepal, C – upper petal of the lateral united petals, D – lower petal of the lateral united petals, E – lower sepal, F – spur, G – peduncle, 1 – total flower length, 2 – length of lower sepal, 3 – width of lower sepal, 4 – length of spur

4. Results

The abundance of the studied populations ranged from 65 to 248 individuals in 2013 and from 68 to 278 individuals – in 2014 (Table 2). Density increased gradually from fallow land, through roadsides and riverbanks, to riparian forest edges (Table 3). Much lower values for this parameter were observed in the willow thicket and forest interior. The height and width of

Table 2. The number of *Impatiens glandulifera* individuals in the studied localities in the years 2013 and 2014

Habitat	Year 2013	Year 2014
Fallow land	65	78
Roadside	82	68
River bank 1	93	72
River bank 2	67	82
Riparian forest edge	248	278
Willow thickets	178	215
Riparian forest interior	67	78

Table 3. The mean (\pm SD) density of *Impatiens glandulifera* individuals in the studied localities in the years 2013 and 2014. The different letters below values indicate significant differences among habitats

Habitat	Year 2013	Year 2014
Fallow land	0.5 (\pm 0.6) ABCDFG	0.6 (\pm 0.6) ABCDFG
Roadside	1.0 (\pm 1.2) ABCDFG	0.9 (\pm 1.0) ABCDEFG
River bank 1	1.0 (\pm 1.3) ABCDEFG	0.8 (\pm 1.2) ABCDFG
River bank 2	0.9 (\pm 1.1) ABCDEFG	1.2 (\pm 0.9) ABCDEFG
Riparian forest edge	2.1 (\pm 1.5) BCDEF	2.3 (\pm 1.3) BDEF
Willow thickets	1.2 (\pm 1.3) ABCDEFG	1.4 (\pm 1.2) ABCDEFG
Riparian forest interior	0.5 (\pm 0.9) ABCDFG	0.6 (\pm 0.8) ABCDFG
The H Kruskal-Wallis test value, <i>P</i>	14.46 $P \leq 0.05$	20.24 $P < 0.01$

stems, number of whorls and side branches, and flower production exhibited similar tendencies (Table 4). The

Table 4. The mean (\pm SD) values of height and width of stems, number of whorls and side branches in *Impatiens glandulifera* individuals in the studied localities. The different letters below values indicate significant differences among habitats

	Fallow land	Roadside	River bank 1	River bank 2	Riparian forest edge	Willow thickets	Riparian forest interior	The H Kruskal-Wallis test value, <i>P</i>
Stem height (cm)	143.0 (\pm 25.8) ABG	151.7 (\pm 25.9) ABFG	186.7 (\pm 61.4) CDEF	207.4 (\pm 47.8) CDE	179.2 (\pm 38.2) CDEF	170.2 (\pm 51.2) BCEF	145.7 (\pm 27.3) ABG	92.2, $P < 0.001$
Stem width (mm)	14.0 (\pm 13.1) AB	15.5 (\pm 15.8) AB	25.1 (\pm 21.1) CDEF	28.9 (\pm 11.2) CDG	35.2 (\pm 25.4) CDE	25.3 (\pm 16.8) CDEF	20.6 (\pm 16.4) DEFG	150.9, $P < 0.001$
No. of whorls	1.1 (\pm 0.4) ABG	1.7 (\pm 0.8) ABG	6.4 (\pm 1.2) CDEF	4.3 (\pm 2.3) CDFG	6.9 (\pm 3.2) CEF	6.2 (\pm 1.7) CDEF	2.4 (\pm 1.5) ABDG	130.6, $P < 0.001$
No. of side branches	2.4 (\pm 1.0) AB	3.5 (\pm 1.8) ABG	14.1 (\pm 7.4) CDEF	11.2 (\pm 5.8) CDEF	13.1 (\pm 6.2) CDEF	11.3 (\pm 4.1) CDEF	4.5 (\pm 3.4) BG	136.8, $P < 0.001$
No. of flowers	13.0 (\pm 7.2) ABG	14.2 (\pm 7.8) ABG	57.9 (\pm 25.1) CDEF	48.7 (\pm 22.9) CDEF	51.5 (\pm 36.0) CDEF	44.4 (\pm 19.5) CDEF	18.0 (\pm 11.6) ABG	127.3, $P < 0.001$

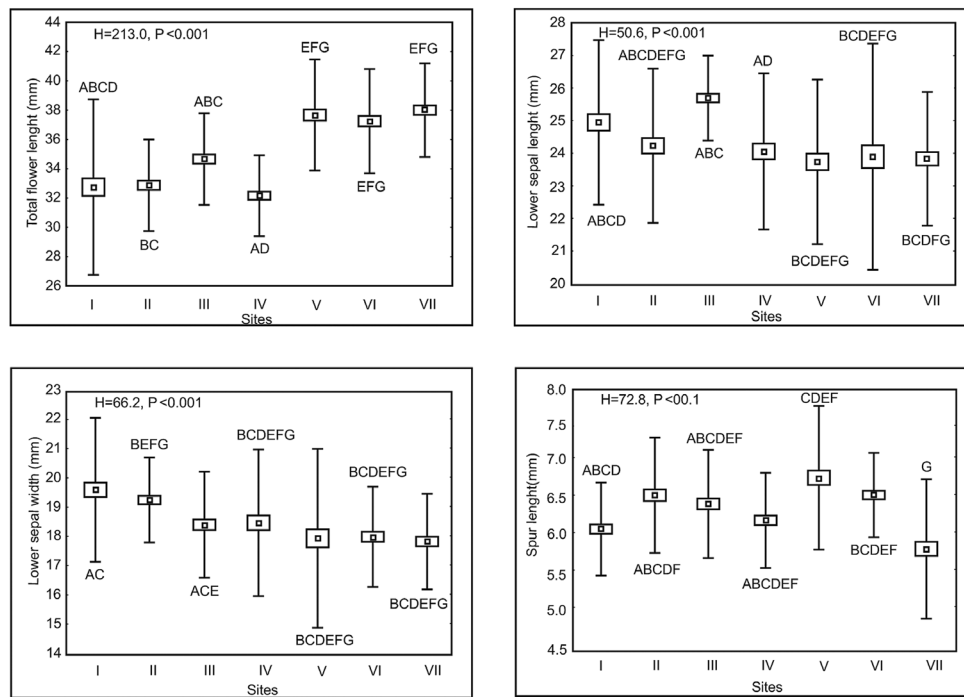


Fig 3. The total length, length and width of lower sepal and length of spur of 100 flowers of *Impatiens glandulifera* in the studied populations. Explanations: I – fallow land, II – roadside, III – river bank 1, IV – river bank 2, V – riparian forest edge, VI – willow thickets, VII – riparian forest interior. Box and whiskers give the mean (square), SE (box) and SD (whiskers). The different letters above/below boxes indicate significant differences among habitats

mean height of stems ranged from 143.0 cm to 179.2 cm from fallow land to the riparian forest edges, respectively, while in the willow thicket and forest interior, it attained 170.2 cm and 145.7 cm, respectively. The average width of stems ranged from 14.0 mm to 35.2 mm from fallow land to the riparian forest edges, respectively, whereas in the willow thicket and forest interior, it measured 25.3 mm and 20.6 mm, respectively. The mean number of whorls ranged from 1.1 to 6.9 from fallow land to the riparian forest edges, respectively, while in the willow thicket and forest interior, it attained 6.2 and 2.4, respectively. The average number of side branches ranged from 2.4 to 13.1 from fallow land to the riparian forest edges, respectively, while in the willow thicket and forest interior, it amounted to 11.3 and 4.5, respectively. The mean number of flowers per stem from the fallow land to the riparian forest edges ranged from 13.0 to 51.5, respectively, whereas in the willow thicket and forest interior, it attained 44.4 and 18.0, respectively.

The average total length of flowers was much lower in populations occurring in the fallow land, at roadsides and along riverbanks, where it ranged from 32.90 to 34.60 mm, than in the riparian forest edges, forest interior, and willow thickets, where it ranged from 37.24 to 37.97 mm (Fig. 3). The dimensions of the lower sepal presented an opposite tendency. The greatest average length of the lower sepal was exhibited by populations located on the fallow land, at roadsides and along riverbanks, where it ranged from 24.12 to 25.67 mm. At

the remaining sites, it ranged from 23.79 to 23.89 mm. Similarly, the greatest width of the lower sepal was exhibited by populations occurring on the fallow land, at roadsides and along riverbanks, ranging from 18.02 to 19.86 mm, while in other locations it measured from 17.79 to 17.92 mm. The length of the spur ranged from 5.85 to 6.80 mm; the highest values were exhibited by individuals growing on the fallow land, the lowest by those growing in the interior of the riparian forest.

5. Discussion

5.1. The abundance of populations

The moderate abundance and density of individuals of *I. glandulifera* occurring on the fallow land and at roadsides might have been caused by the drying out of seeds. This kind of unfavourable influence of water deficiency on population size was previously observed in *Impatiens pallida* (Bennington & McGraw 1995). A considerably higher number of *I. glandulifera* individuals along riverbanks and at the riparian forest edges may have been linked with moderate soil moisture and light availability. The observed decrease in the number of individuals in the willow thicket and forest interior could be attributed to seasonal flooding of the seeds in hollows with stagnant water. The unfavourable effects of stagnant water on the development of individuals of this species were observed by Perrins *et al.* (1993) and Skálová *et al.* (2012).

5.2. Individual traits

The increasing dimensions of stems as well as the number of whorls and branches in *I. glandulifera* from the fallow land through roadsides and riverbanks to riparian forest edges might have been due to the increasing height of adjacent plants and gradual increase of lateral shade. The relatively modest dimensions of *I. glandulifera* individuals observed in the willow thicket and forest inside might have been caused by full shade from above created by trees and shrubs. Moreover, Kostrakiewicz-Gierałt & Zajac (2014) documented that individuals of *I. glandulifera* inhabiting riparian forest interiors achieved modest heights. According to Prach (1994), the inhibition of growth of *I. glandulifera* in forest communities might be due to the plants being entwined by plagiotropic shoots of *Galium aparine*, *Humulus lupulus* and *Calystegia sepium*. The opposite tendency was found by Skálová *et al.* (2013) who recorded greater heights for *I. glandulifera* stems experimentally grown in fully-shaded than in mildly-shaded sites. Moreover, Andrews *et al.* (2005, 2009) observed greater height of *I. glandulifera* individuals in shaded places. A substantial height of stems resulting from considerable shade was also observed in populations of *Impatiens pallida* (Murphy *et al.* 2009) and *Impatiens capensis* (Dudley & Schmitt 1995, 1996; Donohue & Schmitt 1999; Weinig *et al.* 2004).

The observations presented here demonstrating greater flower production in riverbanks and riparian forest edges, than in the fallow land and roadsides may also be due to increased lateral shade. The low level of production of flowers found in populations inhabiting the willow thicket and forest interior might be due to individuals of *I. glandulifera* being overshadowed by trees. This phenomenon does not correspond with the findings of Willis and Hulme (2004) who noted considerably higher reproductive ability in individuals growing in sunny areas than in those inhabiting shady sites. Moreover, the substantial number of flowers in sites characterised by a lower number of neighbouring species was found in *Impatiens capensis* (Schmidt *et al.* 1987; Walters 1996) and *Impatiens parviflora* (Piskorz 2005). At the same time, it is worth mentioning that a survey of selected growth and reproductive characteristics showed that *I. glandulifera* is considered as superior invader comparing to *I. parviflora* (Ugoletti *et al.* 2011).

5.3. Floral traits

The modest total length of flowers and considerable size of lower sepals in *I. glandulifera* recorded on the fallow land, at roadsides and along riverbanks suggest pollination by bumblebees with large thoraxes. The substantial total length of flowers and small dimensions

of lower sepals found in the riparian forest and willow thicket might attract smaller flower visitors. Our observations corresponded with the findings of Bartomeus *et al.* (2010) who documented that *I. glandulifera* individuals growing in open habitats were pollinated chiefly by bumblebees occurring abundantly in floristically rich communities dominated by crops characterised by mass flowering prior to the flowering of *I. glandulifera*. On the other hand, Wilson (1995) documented that the size of flowers in populations of *Impatiens capensis* and *Impatiens pallida* did not lead to differentiation in terms of pollinators. Moreover, Hurlbert *et al.* (1996) suggested that movement of flowers in response to contact with insects might had a greater effect on pollination success than the dimensions of *corollae*.

The observed gradual decrease in the spur length of *I. glandulifera* over successive habitats might contribute to the duration of pollinator visits. The correlation between spur size and curvature, on the one hand, and the duration of pollinator visits, on the other, was observed in *Impatiens capensis* (Young 2008). Nonetheless, Tian *et al.* (2004) documented that the length of the flower spur of *Impatiens reptans* had no effect on pollinator visitation rates. A similar phenomenon was found in *Viola cazorlensis* (Herrera 1990) and *Platanthera lacera* (Little *et al.* 2005). The substantial size of *I. glandulifera* spurs observed in open habitats in the present study may contribute to greater reproductive success. At the same time, it should be added that Vervoort *et al.* (2011) documented that *I. glandulifera* presented large quantities of sucrose-dominant nectar, facilitating pollinator visits. A positive correlation between spur longitude, pollen removal and fruit production was observed in several species such as *Aquilegia pubescens* (Fulton & Hodges 1999), *Dactylorhiza lapponica* (Sletvold *et al.* 2010), *Disa draconis* (Johnson & Steiner 1997) and *Platanthera bifolia* (Boberg & Ågren 2009; Boberg *et al.* 2013).

6. Conclusions

The increase in the stem dimensions and number of branches in individuals of *I. glandulifera* from the fallow land to riparian forest edges may result in a gradual increase in competitive abilities enabling the use of resources. The increasing production of flowers achieving modest total lengths and the considerable dimensions of the lower sepal and spur may contribute to the augmentation of opportunities for successful pollinator visits in open sites.

The relatively smaller dimensions of stems, the low level of production of flowers attaining greater length, and the modest dimensions of the lower sepal and spur seem sufficient to enable the maintenance of populations in closed habitats.

References

- ANDREWS M., MAULE H. G., HODGE S., CHERRILL A. & RAVEN J. A. 2009. Seed dormancy, nitrogen nutrition and shade acclimation of *Impatiens glandulifera*: implications for successful invasion of deciduous woodland. *Plant Ecology and Diversity* 2(2): 145-153. <http://dx.doi.org/10.1080/17550870903186256>
- ANDREWS M., MAULE H. G., RAVEN J. A. & MISTRY A. 2005. Extension growth of *Impatiens glandulifera* at low irradiance: importance of nitrate and potassium accumulation. *Ann. Bot.* 95: 641-648.
- BALOGH L. 2008. Himalayan balsam (*Impatiens glandulifera* Royle). In: Z. BOTTA-DUKÁT & L. BALOGH (eds.). The most important invasive plants in Hungary, pp: 129-137. Institute of Ecology and Botany, Hungarian Academy of Sciences, Vácrátót, Hungary.
- BENNINGTON C. C. & MCGRAW J. C. 1995. Natural selection and ecotypic differentiation in *Impatiens pallida*. *Ecol. Monogr.* 65(3): 303-324. <http://dx.doi.org/10.2307/2937062>
- BARTOMEUS I., MONTERRAT VILÀ M. & STEFFAN-DEWENTER I. 2010. Combined effects of *Impatiens glandulifera* invasion and landscape structure on native plant pollination. *J. Ecol.* 98: 440-450. <http://dx.doi.org/10.1111/j.1365-2745.2009.01629.x>
- BERLING D. J. & PERRINS J. M. 1993. *Impatiens glandulifera* Royle (*Impatiens roylei* Walp.). *J. Ecol.* 81: 367-382.
- BOBERG E. & ÅGREN J. 2009. Despite their apparent integration, spur length but not perianth size affects reproductive success in the moth-pollinated orchid *Platanthera bifolia*. *Funct. Ecol.* 23: 1022-1028. <http://dx.doi.org/10.1111/j.1365-2435.2009.01595.x>
- BOBERG E., ALEXANDERSSON R., JONSSON M., MAAD J., ÅGREN J. & NILSSON L. A. 2013. Pollinator shifts and the evolution of spur length in the moth-pollinated orchid *Platanthera bifolia*. *Ann. Bot.* 113(2): 267-275. <http://dx.doi.org/10.1093/aob/mct217>
- CHMURA D., CSONTOS P. & SENDEK A. 2013. Seed mass variation in central European populations of invasive *Impatiens glandulifera* Royle. *Polish J. Ecol.* 61(4): 805-809.
- CLEMENTS D. R., FEENSTRA K. R., JONES K. & STANFORTH R. 2008. The biology of invasive alien plants in Canada. 9. *Impatiens glandulifera* Royle. *Can. J. Plant Sci.* 88(2): 403-417. <http://dx.doi.org/10.4141/CJPS06040>
- DONOHUE K. & SCHMITT J. 1999. The genetic architecture of plasticity to density in *Impatiens capensis*. *Evolution* 53(5): 1377-1386. <http://dx.doi.org/10.2307/2640884>
- DREWNIAK M., ŻYLA M. & WÓJCIK S. 2007. Gleby. In: I. JĘDRYCHOWSKI (ed.). Atlas otoczenia Kampusu 600-lecia Odnowienia Uniwersytetu Jagiellońskiego, pp. 46-47. Uniwersytet Jagielloński, Instytut Geografii i Gospodarki Przestrzennej.
- DUBIEL E. & SZWAGRZYK J. (eds.) 2008. Atlas roślinności rzeczywistej Krakowa. 159 pp. Urząd Miasta Krakowa, Wydział Kształtowania Środowiska, Kraków.
- DUDLEY S. A. & SCHMIDT J. 1995. Genetic differentiation in morphological responses to simulated foliage shade between populations of *Impatiens capensis* from open and woodland sites. *Funct. Ecol.* 9(3): 655-666. <http://dx.doi.org/10.2307/2390158>
- DUDLEY S. A. & SCHMIDT J. 1996. Testing the adaptive plasticity hypothesis: Density-dependent selection on manipulated stem length in *Impatiens capensis*. *Amer. Nat.* 147: 445-465. <http://dx.doi.org/10.1086/285860>
- FULTON M. & HODGES S. A. 1999. Floral isolation between *Aquilegia formosa* and *Aquilegia pubescens*. *Proc. Royal Soc. B: Biol. Sci.* 266 (1435): 2247-2252. <http://dx.doi.org/10.1098/rspb.1999.0915>
- GRUNTMAN M., PEHL A. K., JOSHI S. & TIELBOERGER K., 2014. Competitive dominance of the invasive plant *Impatiens glandulifera*: using competitive effect and response with a vigorous neighbour. *Biological Invasions* 16(1): 141-151. <http://dx.doi.org/10.1007/s10530-013-0509-9>
- HEJDA M. & PYŠEK P. 2006. What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation? *Biol. Conserv.* 132(2): 143-152. <http://dx.doi.org/10.1016/j.biocon.2006.03.025>
- HEJDA M., PYŠEK P. & JAROŠÍK V. 2009. Impact of invasive plants on the species richness, diversity and composition of invaded communities. *J. Ecol.* 97(3): 393-403. <http://dx.doi.org/10.1111/j.1365-2745.2009.01480.x>
- HERRERA C. M. 1990. The adaptedness of the floral phenotype in a relict endemic, hawkmoth-pollinated violet. 1. Reproductive correlates of floral variation. *Biol. J. Lin. Soc.* 40: 263-274.
- HURLBERT A. H., AKI HOSOI S., TÉMELES E. J. & EWALD P. W. 1996. Mobility of *Impatiens capensis* flowers: Effect on pollen deposition and hummingbird foraging. *Oecologia* 105: 243-246.
- HULME P. E. & BREMNER E. T. 2007. Assessing the impact of *Impatiens glandulifera* on riparian habitats: partitioning diversity components following species removal. *J. Appl. Veg.* 43(1): 43-50. <http://dx.doi.org/10.1111/j.1365-2664.2005.01102.x>
- JOURET M. F. 1977. Effect on gibberellic-acid on dormancy breaking of *Impatiens parviflora*, *Impatiens glandulifera* and *Impatiens balfourii* seeds. *Bulletin de la Société Royale de Botanique Belgique* 110(1-2): 113-118.
- JOHNSON S. D. & STEINER K. E. 1997. Long-tongued fly pollination and evolution of floral spur length in the *Disa draconis* complex (Orchidaceae). *Evolution* 51(1): 45-53.
- KOLLMANN J. & BAÑUELOS M. J. 2004. Latitudinal trends in growth and phenology of the invasive alien plant *Impatiens glandulifera* (Balsaminaceae). *Diversity Distrib.* 10: 377-385.
- KONDRACKI J. 2000. *Geografia regionalna Polski*. 440 pp. PWN, Warszawa.
- KOSTRAKIEWICZ-GIERALT K. & ZAJĄC M. 2014. The influence of habitat conditions on the performance of two invasive, annuals — *Impatiens glandulifera* and *Bidens frondosa* *Biologia* 69(4): 449-462. <http://dx.doi.org/10.2478/s11756-014-0333-4>
- MURPHY G. P. & DUDLEY S. A. 2009. Kin recognition: Competition and cooperation in *Impatiens* (Balsaminaceae). *Am. J. Bot.* 96(11): 1990-1996. <http://dx.doi.org/10.3732/ajb.0900006>
- LAMBON P. W., PYŠEK P., BASNOU C., HEJDA M., ARIANOUTSOU M., ESSL F., JAROŠÍK V., PERGL J., WINTER M. ANASTASIU

- P., ANDRIOPOULOS P., BAZOS I., BRUNDU G., CELESTIGRAPOW L., CHASSOT P., DELIPETROU P., JOSSEFSON M., KARK S., KLOTZ S., KOKKORIS Y., KÜHN I., MARCHANTE H., PERGLOVÁ I. PINO J., VILÁ, ZIKOS A., ROY D. B. & HULME P. E. 2008. Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs. *Preslia* 80: 101-149.
- LITTLE K. J., DIERINGER G. & ROMANO M. 2005. Pollination ecology, genetic diversity and selection on nectar spur length in *Platanthera lacera* (Orchidaceae). *Plant Species Biology* 20(3): 183-190. <http://dx.doi.org/10.1111/j.1442-1984.2005.00137.x>
- MACK R. N., SIMBERLOFF D., LONSDALE W. M., EVANS H., CLOUT M. & BAZZAZ F. A. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecol Appl* 10: 689-710. [http://dx.doi.org/10.1890/1051-0761\(2000\)010\[0689:bicegc\]2.0.co;2](http://dx.doi.org/10.1890/1051-0761(2000)010[0689:bicegc]2.0.co;2)
- NIENHUIS C. M. & STOUT J. C. 2009. Effectiveness of native bumblebees as pollinators of the alien invasive plant *Impatiens glandulifera* (Balsaminaceae) in Ireland. *Journal of Pollination Ecology* 1(1): 1-11.
- PERRINS J., FITTER A. & WILLIAMSON M. 1993. Population biology and rates of invasion of three introduced *Impatiens* species in the British Isles. *J. Biogeogr.* 20: 33-44.
- PISKORZ R. 2005. The effect of oak-hornbeam diversity on flowering and fruiting of *Impatiens parviflora*. *Rocz. AR. Pozn. CCCLXXIII Bot-Stec.* 9: 187-196.
- PRACH K. 1994. Seasonal dynamics of *Impatiens glandulifera* in two riparian habitats in central England. In: DE WAAL L. C. (ed.). *Ecology and management of invasive riverside plants*, pp 127-133. John Wiley Sohns, Chichester.
- JAROŠÍK V., HULME P. E., PERGL J., HEJDA M., SCHAFFNER U. & VILÁ M. 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Global Change Biology* 18: 1725-1737. <http://dx.doi.org/10.1111/j.1365-2486.2011.02636.x>
- SCHMIDT J., ECCLESTON J. & EHRHARDT D. W. 1987. Density-dependent flowering phenology, outcrossing, and reproduction in *Impatiens capensis*. *Oecologia* 72(3): 341-347. <http://dx.doi.org/10.1007/BF00377561>
- SKÁLOVÁ H., JAROŠÍK V., DVOŘÁČKOVÁ S. & PYŠEK P. 2013. Effect of intra- and interspecific competition on the performance of native and invasive species of *Impatiens* under varying levels of shade and moisture. *Plos One* 8(5): e62842. [10.1371/journal.pone.0062842](http://dx.doi.org/10.1371/journal.pone.0062842)
- SKÁLOVÁ H., HAVLIČKOVÁ V. & PYŠEK P. 2012. Seedling traits, plasticity and local differentiation as strategies of invasive species of *Impatiens* in Central Europe. *Ann. Bot.* 110(7): 1429-1438. <http://dx.doi.org/10.1093/aob/mcr316>
- SKIBA S., DREWNIK M., KACPRZAK A., ŻYŁA M. & ŻELAZOWSKA E. 2005. Pokrywa glebowa rejonu Kampusu Uniwersytetu Jagiellońskiego. In: B. DOMAŃSKI & S. SKIBA (eds.). *Geografia i Sacrum*, I, pp. 161-169. Instytut Geografii i Gospodarki Przestrzennej, Kraków.
- SLETVOLD N., GRINDELAND J. M. & ÅGREN J. 2010. Pollinator-mediated selection on floral display, spur length and flowering phenology in the deceptive orchid *Dactylorhiza lapponica*. *New Phytol.* 188(2): 385-92. <http://dx.doi.org/10.1111/j.1469-8137.2010.03296.x>
- TANNER R. A., VARIA S., ESCHEN R., WOOD S., MURPHY S. T. & GANGE A. C. 2013. Impacts of an invasive non-native annual weed, *Impatiens glandulifera*, on above- and below-ground invertebrate communities in the United Kingdom. *PlosOne* 8(6): e67271. <http://dx.doi.org/10.1371/journal.pone.0067271>
- TIAN J., LIU K. & HU G. 2004. Pollination ecology and pollination system of *Impatiens reptans* (Balsaminaceae) endemic to China. *Ann. Bot.* 93: 167-175. <http://dx.doi.org/10.1093/aob/mch013>
- TITZE A. 2000. The efficiency of insect pollination of the neophyte *Impatiens glandulifera* (Balsaminaceae). *Nord. J. Bot.* 20: 33-42.
- UGOLETTI P., STOUT J. C. & JONES M. B. 2011. Ecophysiological traits of invasive and noninvasive introduced *Impatiens* species. *Proceedings of the Royal Irish Academy* 111(3): 1-14. <http://dx.doi.org/10.3318/BIOE.2011.12>
- WALTERS B. B. 1996. Effect of canopy gaps and flower patch size on pollinator visitation of *Impatiens capensis*. *Bulletin of the Torrey Botanical Club* 123(3): 184-188.
- WEING C., GRAVUER K. A., KANE N. C. & SCHMITT J. 2004. Testing adaptive plasticity to UV: costs and benefits of stem elongation and light-induced phenolics. *Evolution* 58(12): 2645-2656. <http://dx.doi.org/10.1554/03-675>
- WILLIS S. G. & HULME P. E. 2004. Environmental severity and variation in the reproductive traits of *Impatiens glandulifera*. *Funt. Ecol.* 18: 887-898. <http://dx.doi.org/10.1111/j.0269-8463.2004.00907.x>
- WILSON P. 1995. Selection for pollination success and the mechanical fit of *Impatiens* flowers around bumblebee bodies. *Biol J Linn Soc* 55: 355-383.
- WINTER M., SCHWEIGER O., KLOTZ S., NENTWIG W., ANDRIOPOULOS P., ARIANOUTSOU M., BASNOU C., DELIPETROU P., DIDZIULIS V., HEJDA M., HULME P. E., LAMBDOON P. W., PERGL J., PYŠEK P., ROY D. B. & KUHN I. 2009. Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. *Proc. Nat. Acad. Sci. USA* 106: 21721-21725. <http://dx.doi.org/10.1073/pnas.0907088106>
- VITOUSEK P. M., D'ANTONIO C. M., LOOPE L. L. & WESTBROOKS R. 1996. Biological invasions as global environmental change. *Am Sci* 84: 468-487.
- VERVOORT A., CAWOY V. & JACQUEMART A. L. 2011. Comparative reproductive biology in occurring invasive and native *Impatiens* species. *Int. J. Plant Sci.* 172(3): 366-377. <http://dx.doi.org/10.1086/658152>
- YOUNG H. I. 2008. Selection on spur shape in *Impatiens capensis*. *Oecologia* 156: 535-543. <http://dx.doi.org/10.1007/s00442-008-1014-1>
- ZYBARTAITĖ L., ZUKAUSKIENE J., JODINSKIENE M., JANSSENS S. B., PAULASKAS A. & KUPCINSKIENE E. 2011. RAPD analysis of genetic diversity among Lithuanian populations of *Impatiens glandulifera*. *Žemdirbystė-Agriculture* 98(4): 391-398.